

THE BIOLOGICAL BULLETIN

PUBLISHED BY THE MARINE BIOLOGICAL LABORATORY

PIGMENT MIGRATION IN THE EYES OF THE MOTH, *EPHESTIA KUEHNIELLA* ZELLER

M. F. DAY

(From the Biological Laboratories, Harvard University)

INTRODUCTION

The movement of pigment in the eyes of insects has been described many times, but there is little information in the literature suggesting what factors are involved in bringing about this movement. In certain Crustacea it has been conclusively demonstrated (Kleinholz, 1936, 1938; Welsh, 1939, 1941) that the movement of the pigment from the "dark" position into the "light" position is dependent upon the action of a hormone secreted by the eye stalk. In view of recent discoveries of reciprocal effects between insect and crustacean hormones (Hanström, 1937; Brown and Meglitsch, 1940), the question arises as to whether endocrines also regulate pigment migration in the moth eye. There are at least three ways in which eye pigment migration in an insect might be controlled, namely, by hormones, by nerves, and by the action of the pigment cells as independent effectors. Possibly also a combination of these three methods of control might be found in some insects.

Many of the early workers (see Demoll, 1911) believed that the control was nervous in nature. But the experiments of Exner and Demoll (*cf.* review by Parker, 1932), and the subsequent work of Uchida (1934) on the long-horned grasshopper, indicated that the movement was generally slow in comparison with most nervous responses. Friza (1928) suggested, as a result of his study of *Mantis religiosa*, that the movement was humorally controlled. In addition, the work of Horstmann (1935), in which he corroborated the conclusions of the older workers on the existence of a diurnal rhythm in pigment migration under constant conditions of the external environment, indicates that the response is not that of independent effectors, in which the pigment cells respond directly to light. Collins (1934), however, concluded that it was most likely that light acted directly on the pigment cells of the moth, *Carpocapsa*.

In the following experiments, the movement of the eye pigment of the moth, *Ephestia kuehniella* Zeller, will be described, and an attempt

made to determine which of the three above-mentioned factors is responsible for the movement. The study is based on the examination of serial sections of the heads of over 450 moths.

The moths were bred in large glass jars, each containing about two inches of dry oatmeal. Under these conditions the life-cycle occupied about six weeks, a plentiful supply of adult moths thus being available at all times. Observations were made on sections of entire heads fixed in alcoholic Bouin's fluid, which penetrated with sufficient rapidity that no migration of pigment occurred. Results were comparable in this regard with those obtained with fixation by hot water, but histological preservation was better. Some sections were stained in Mallory's triple stain or impregnated by Bodian's protargol method, and others were depigmented in Grenacher's fluid, and subsequently stained or impregnated.

It is a pleasure to thank Professor J. H. Welsh and Dr. L. H. Kleinholtz for suggestions during the course of this work.

ANATOMICAL CONSIDERATIONS

Umbach (1934) described the eye structure of *Ephestia* in detail. The following description will therefore deal only with the pigment cells and other points which directly concern our discussion. Features of a single ommatidium are shown in Fig. 1.

The pigment in the eye is arranged in three distinct groups, but attempts to homologize these with the pigment cells of Crustacea were unsuccessful. One group of pigment granules surrounds the bases of the rhabdoms and also extends below the basement membrane. Umbach (1934) has shown that this pigment in *Ephestia* is not contained in specific retinal pigment cells, as it is in many insects. Although in *Ephestia* the pigment is never completely withdrawn beneath the basement membrane, as in *Vanessa* (Demoll, 1917), it apparently exhibits some movement. But the extent of this movement does not exceed ten microns, and no attempt has been made to determine its cause.

A second group of pigment granules is contained in cells which have a varied terminology. They are here called primary pigment cells, but have been referred to as iris pigment cells by Snodgrass (1935), as primary iris cells by Wigglesworth (1939), distal pigment cells by Collins, and accessory pigment cells by Uchida. These cells closely surround the crystalline cones. The nuclei are extremely flattened, and the pigment granules are arranged in a thin layer around the cones. Neither these cells nor their pigment granules have been observed to migrate. Finally, the large accessory pigment cells (secondary iris cells, Wigglesworth; principal pigment cells, Uchida) are very conspicuous

and contain most of the pigment granules. The entire cell moves, as well as the pigment granules contained in it, for the nuclei have been shown in depigmented preparations to have moved through a distance of about 30 microns, with the mid-point at about the proximal end of

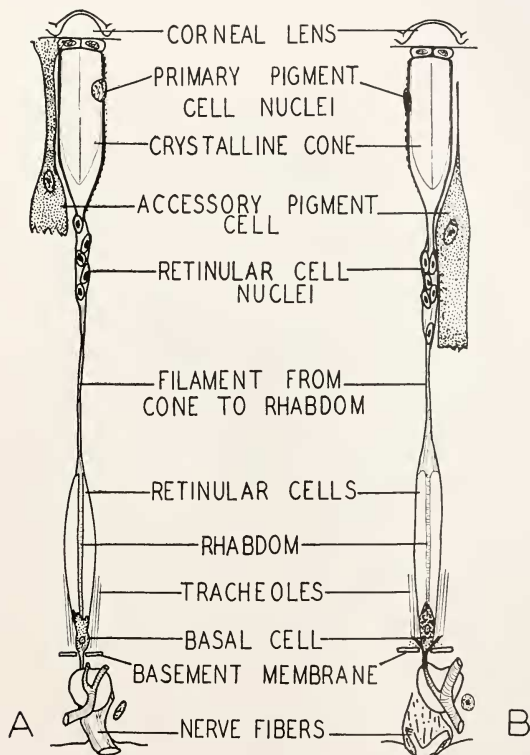
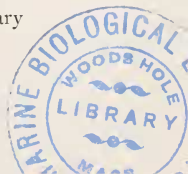


FIG. 1. Longitudinal sections of two ommatidia from eyes of *Ephestia* in (a) dark-adapted, and (b) light-adapted positions, respectively.

the crystalline cone. None of the pigment in the eyes of *Ephestia* has a reflecting function.

Another important aspect of the structure of the eye is the size of the ommatidia. Umbach (1934) states that there are between 2,000 and 2,500 in each eye. Between 60 and 70 of these are seen in each eye in a transverse section of the head (Fig. 2). The ommatidia vary



in size, the smallest being on the dorsal side, and the largest on the ventral side of the eye, the difference between the two extremes being about 20 per cent of their length. The accessory pigment cells migrate a greater distance in the larger ommatidia than they do in the smaller ones, as in Crustacea, where the greatest amount of migration occurs in the largest ommatidia which are found on the dorsal side of the eye.



FIG. 2. Transverse section of part of head of *Ephesia*, showing the arrangement and differences in size of the ommatidia. Pigment cells in light-adapted position.

These differences make it necessary to select the central ommatidia for comparisons between eyes of insects treated in different ways. Also, the eyes of female moths are on the average slightly larger than those of males. The average length of the central ommatidia of ten males, measured from the basement membrane to the distal end of the crystalline cone, was 177.3 microns, while that from ten females was 186.8 microns, longer than the average of the males by 5 per cent. Therefore

insects of only one sex were used in experiments when they were to be directly compared.

Two other details of anatomy should be mentioned. The first is that no contractile fibers, such as were demonstrated by Welsh (1930) in the eyes of *Palaemonetes*, have been seen in the eyes of *Ephestia*. Movement of pigment granules and of the pigment cells probably results, as was suggested by Bennitt (1924), and Parker (1932), from protoplasmic streamings or surgings, and a similar mechanism will probably explain the interesting movement (first demonstrated by Umbach) of the reticular cells themselves. Finally, Bodian preparations of both pigmented and depigmented eyes showed no sign of effector nerves supplying the accessory pigment cells. The significance of such negative evidence is, however, questionable in view of the difficulty of demonstrating nerves to sense hairs which occur in large numbers on the eyes of some insects.

NORMAL MOVEMENT OF THE ACCESSORY PIGMENT CELLS

The normal movement of the accessory pigment cells, such as occurs when a dark-adapted moth is exposed to light, can be followed by referring to Fig. 3. First, it is to be noticed that the extreme dark position, as seen in *A*, is rarely found. Moths kept for several days in the dark more frequently have their accessory pigment cells in a position similar to that in *B*. In this stage pigment granules are evenly distributed and extend from the level of the distal ends of the cones to about 15 microns beneath their proximal ends, the level of the grouped reticular cell nuclei. The first movement of pigment in such an eye usually becomes evident as an increasing aggregation of the granules in the proximal part of the cells. This region of the cell then moves proximally toward the basement membrane (Fig. 3, *D*), accompanied by a simultaneous decrease in the size of the extensions of the pigment cells between the cones. As the proximal movement continues these extensions become attenuated (Fig. 3, *E*), and the characteristic "frayed" region at the distal end is eventually withdrawn (Fig. 3, *F*). Between the two last-mentioned stages, movement of the pigment cell nuclei occurs. The final stage of movement involves the almost complete withdrawal of granules of the accessory pigment cells from between the cones (Fig. 3, *G*). Light alone is incapable of causing greater proximal movement than that seen in Fig. 3, *G*, but certain treatments described below may induce more extensive movement.

The movement in *Ephestia* is not so simple a migration as was indicated by Collins (1934, Pl. 4) in *Carposapsa*. Measurements of the distance of the pigment cells from the cones do not indicate all the

changes that occur, since two types of movement, lateral as well as longitudinal, are found. These are seen in stages *E* and *F*, and are equivalent to those observed by Peabody (1939) in the isopod, *Idothea*. The fact, well known in Crustacea, that the type of pigment migration varies in different species, holds also for insects.

EXPERIMENTAL RESULTS

Diurnal Rhythm

The first experiments were made to determine whether a persistent diurnal rhythm existed in the movement of the pigment cells, as previously recorded for many insects and Crustacea (for review, see Welsh, 1939). In *Ephestia*, kept under constant illumination for four days, the pigment cells were found in the light-adapted position at any hour of the day or night. Likewise, insects kept in darkness, with all other usually controlled factors maintained constant, had pigment cells in the dark position during both day and night. This is believed to be the first reported absence of a persistent diurnal rhythm in a moth. However, in view of the marked interspecific differences recorded by Welsh (1935), even within a single genus of crustaceans, and the absence of diurnal rhythm of pigment migration in *Palaeomonetes* (Kleinholz, 1936), the differences between various insects are perhaps not so surprising.

The majority of previous workers on Lepidoptera have made their observations on the changes of the pseudopupil, or on the presence of glow in the eye when illuminated at night. It has rarely been possible to demonstrate glow during the day. In *Ephestia* in constant darkness the eyes glow during the day as well as at night. The glow, however, disappears rapidly upon illumination,—as shown for other insects by many observers (see Merker, 1929). At a light intensity of 12 ft-candles, 1 to 2 minutes are required for the glow to disappear from dark-adapted *Ephestia* at 25° C. Sections of eyes which exhibited glow and those from which it had just disappeared show that the changes in position of the pigment cells are frequently almost imperceptible. Glow in *Ephestia* is not caused by reflecting pigment, as in some Crustacea, nor does it seem likely that its appearance is due to the reflection of light from the tracheal tapetum between the rhabdoms. The cause of glow in insects deserves further study.

The Effect of Light

Intensity.—The effect of light of various intensities was determined. A standard source (15-watt Mazda bulb, filtered through Wratten Neutral Filter) was maintained at a constant distance from a group of insects which were inclosed, as in all subsequent experiments, in thin,

2-dram glass vials, plugged with cotton wool, and standing, bottom uppermost, in a container with white walls. All experiments were begun with an excess of moths, and insects which were persistently active, or which were settled facing away from the light, were not used. It was soon found that several factors had to be controlled in order to obtain consistent results. Since it seemed that the rate of response was influenced by the age of the moths, only newly emerged virgins were used. A further complication was found in some moths due to the presence of a parasite. In such cases many spores were found in sections of the head, usually in the hemocoel, but sometimes also in the tissues. Such individuals were not considered in the experiments.

Light intensity was varied by accurately calibrated neutral filters. The results are indicated in Fig. 4. In this method of presenting data, the technique employed involves measuring the pigment migration of a number of individuals (in this case, five), and then photographing an eye whose measurement is nearest the average. After 30 minutes exposure to an intensity of approximately 0.3 ft-candles, migration into the light position is incomplete. Above 3 ft-candles a maximum response is produced in the same period of time. While these results are readily reproducible, single measurements of proximal migration are insufficient to permit a determination of the exact type of relationship between intensity of light and distance migrated. In all subsequent experiments an intensity of 12 ft-candles was employed.

The Rate of Movement.—The next step was to determine the time taken for the migration of the pigment cells in both directions, when intensity, temperature, and other factors were kept constant. The only method which is available in the case of *Ephesia* is to fix and section eyes of moths which have been exposed to light for varying periods of time. Since this method has been shown by Welsh (1930) to be unsatisfactory in comparison with methods of direct observation which are applicable to animals with stalked eyes, the times given below can only be considered to indicate the approximate rates.

The results of one experiment are recorded in Fig. 3 (B-G). Under the conditions of the experiment, movement could be demonstrated within one and one-half minutes after the exposure of the moths to light. Movement was most rapid between 4 and 7 minutes, and was completed within approximately 12 minutes. If, after 30 minutes, the light is removed, dark adaptation begins within 5 minutes, but takes somewhat longer for completion than movement under the influence of light, a conclusion in agreement with that of all previous workers on Crustacea and insects. In these experiments movement back to the dark position required about 20 minutes.

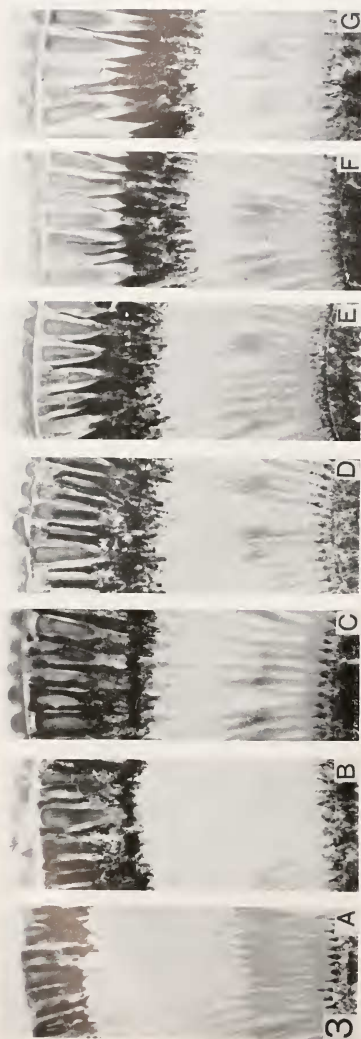


PLATE I

3. Movement of accessory pigment cells in the eyes of *E. plecostia* on exposure to light. (A) Extreme dark position, (B) Usual dark position, (C) 0.5 min. light, (D) 3.0 min. light, (E) 5.0 min. light, (F) 8.0 min. light, (G) 10.0 min. light.
4. The effect of light intensity. (A) 0.3 ft-candles, (B) 3.0 ft-candles.
5. Movement of only those pigment cells associated with illuminated onomatidia, when most of the eye is covered by an opaque mixture.

The Effect of Localized Light.—In the experiments of Bennitt (1932) exposure of only a small region of one eye of a crayfish resulted in pigment migration in all ommatidia of that eye and of the other eye as well. Comparable experiments were performed with etherized *Ephestia* by covering both eyes except for a few ommatidia of one eye with the opaque mixture recommended by Crozier, Wolf, and Zerrahn-Wolf (1937). These moths were allowed to recover in the dark, and after 24 hours were exposed to 12 ft-candles for 20 minutes. Under these conditions the sectioned eyes frequently showed that only the region which had been exposed to the light exhibited pigment migration (Fig. 5). Bennitt's results would be expected on the basis of the humoral theory of control of migration. The ease with which it is possible to obtain unequal movement of different pigment cells in the same eye in *Ephestia* suggests that the humoral theory of control may not be applicable in this case. That other insects may react in a manner similar to *Ephestia* has been indicated by the work of Exner (1891) and Demoll (1911).

The Effect of Temperature

Rate of Migration.—Experiments exactly simulating those reported above on the rate of migration under constant light intensity were performed at a temperature of 12.5° C. instead of at 25° C. It was found that in the dark the pigment cells were extended over a greater distance proximally at 12.5° C. than at 25° C. (Fig. 6). However, movement of the pigment cells during light adaptation was in no way different at the lower temperature, except that they did not have so far to travel before reaching the light position. The indications are, then, that the processes of movement have a temperature coefficient of 1.0 within the range 12.5 to 25° C. (but compare the results of Bennitt (1924) on *Gammarus*).

Extremes of Temperature.—When the factor of temperature was found to have an effect on the position of the pigment cells in darkness, a series of experiments was performed to determine the effects of more extreme temperatures. Moths were placed in light-tight containers at temperatures of 3°, 5°, 10°, 12.5°, 25°, and 37° C. for two hours. The moths at the lowest temperature became immobile and those at 37° were extremely active. All were living, however, and were fixed in the dark. Sections showed that the eyes of moths at temperatures from 10° to 25° were in the normal dark-adapted position. At 3°, however, there was considerable movement toward the light position, while at 37° the pigment cells were concentrated between the cones, thus showing a more complete dark adaptation than is ever found under normal tem-

peratures (Fig. 7). This demonstrates for *Ephestia* a conclusion reached long ago for Crustacea by Congdon (1907), that low temperature produces the same effect as light, and that high temperature has an opposite effect. In view of this latter finding, the result of two mutually opposite stimuli was investigated by exposing moths to a temperature of 37° C. and a light intensity of 12 ft-candles at the same time. Under these conditions the effect of light predominated over the effect of heat in nine cases. However, in one moth, where the thresholds must have been approximately equalized, some of the pigment cells migrated into the extreme light position, while others migrated only slightly (Fig. 8). Interestingly enough, corresponding ommatidia in both eyes exhibited the same response, suggesting the possibility of a central control.

The amount of proximal migration produced in the dark by low temperature is greater in the ommatidia on the ventral side of the eye than in those on the dorsal side, as is the case in light adaptation at normal temperatures. The suggestion that such differences in the light-adapted eye are due to differences in the amount of light reaching each ommatidium is therefore untenable.

The Effect of Mechanical Stimulation

The rather unexpected effect of shaking which Horstmann (1935) reported on the phototactic responses of moths has been substantiated with *Ephestia*. If a vial containing a moth is held toward the light and is tapped lightly, the moth exhibits a marked negative response. If the tapping is continued for about 15 seconds the moth will suddenly turn, progress towards the light, and is thereafter strongly positively phototactic. Sections were made of both light and dark-adapted *Ephestia*

PLATE II

EXPLANATION OF FIGURES

6. The effect of temperature, showing spreading of pigment granules after 1 min. in light at 12.5° C.
7. The effect of (A) darkness and 3° C., (B) light and 37° C.
8. Irregular movement of pigment cells induced by simultaneous action of high temperature (37° C.) and light (12 ft-candles).
9. The effect of anaesthetization by ether. Note the clumping of pigment granules.
10. The effect of the injection of chloretone, inducing greater movement into the light position than is ever produced by light alone.
11. The irregular movement into the light position induced by high tensions of carbon dioxide.
12. Transverse section of the head, illustrating the effect of severing the left optic tract. Pigment in the left eye is in the light position, while that in the eye on the uninjured side is in the dark position.



6



7

A

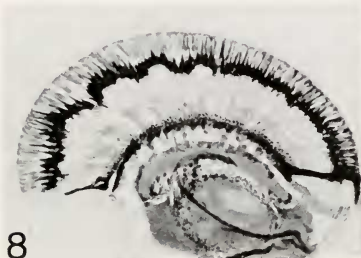


8

B



9



10



11



12



13

before and after shaking, and of those which were positively and negatively phototactic. It was found that shaking had no demonstrable effect on the position of the accessory pigment cells, nor was there any effect of shaking on the rate of disappearance of glow. Conversely, glow could not be made to reappear just after its disappearance by any kind of mechanical stimulation. We can only conclude that in the case of *Ephestia* differences in phototactic response are not necessarily correlated with obvious changes in the position of the pigment cells.

The Effects of Certain Drugs, Anaesthetics, and Extracts

Methods.—Injections of approximately 0.001 ml. of fluid were made into the thorax of moths by the microinjection method of Ephrussi and Beadle (1936). Anaesthetization and injection, which occupied between one and two minutes, were performed in dim light. The moths were then kept 15 to 20 minutes in darkness before fixing the eyes. Since it was possible that some of the injected substances might cause movement into the dark position, some of the injected animals were exposed to light.

Ether.—In concentrations just sufficient to anaesthetize a moth, ether has the effect of sending the pigment even further into the dark position than dark alone. A secondary effect is noted when moths are exposed to ether for longer periods of time. The pigment cells are then apparently disorganized, and have a slight tendency even to move proximally in an irregular fashion. The pigment granules may assume a clumped appearance (Fig. 9). The illumination of moths which are under the influence of either of these effects results in apparently normal proximal movement.

Chloretone.—Injection of substances causing proximal migration of pigment cells will obscure the effects of ether. When a saturated aqueous solution of chloretone is injected into a dark-adapted moth, the pigment cells will migrate into the light position, even though the moths are kept in the dark. Usually the movement will be comparable to that produced by light, but sometimes the distance migrated is greater than is ever produced by light alone (Fig. 10). Chloretone might inhibit nerve impulses which would result in maintaining the pigment in the dark position. This inhibition could be exerted either upon motor nerves or on nerves innervating an incretory organ. A similar criticism can be made of any experiments with anaesthetics or drugs.

The Effects of Adrenalin, Acetylcholine, and Prostigmin.—If movement of pigment cells is under the control of the nervous system, it might be expected that the application of appropriate chemical mediators

would result in their response. Adrenalin and acetylcholine have both been extracted from insects (von der Wense, 1938; Corteggiani and Serfaty, 1939) but the existence of an adrenergic or cholinergic system has not been proved. The injection, with appropriate controls, of dilutions of 1:1,000 and 1:10,000 adrenalin, and 1:10,000 and 1:100,000 acetylcholine produced no change in the position of the pigment cells. Prostigmin, though having some of the effects on behavior of *Ephestia* comparable to those described for eserine in the mantis by Roeder (1939), did not influence the pigment cells.

Head Extract.—Experiments comparable to certain of those of Kleinholz (1936) were performed on *Ephestia*. The heads of ten light-adapted moths were triturated in 1 ml. of insect Ringer. The extract was boiled, cooled, and injected in the manner described above. Neither this concentration of the extract, nor a dilution of one part of extract to five of Ringer, produced any proximal migration of the pigment cells when the insects were kept in the dark. Nor did such injections inhibit movement when they were exposed to light.

Sinus Gland Extract.—The sinus glands of three specimens of *Uca pugilator* were ground in 0.5 ml. of insect Ringer. The extract was boiled, cooled, and injected into dark-adapted moths. The results were negative, as with extracts of *Ephestia*.

The Effect of High Tensions of Carbon Dioxide.—The striking anaesthetic effect of carbon dioxide on insects has been known for a long time. In *Ephestia* carbon dioxide produces a proximal migration greater than is ever produced by light alone. But this movement is not uniform, so that all cells do not react to exactly the same extent (Fig. 11). The effect on the position of the pigment is still marked after 20 minutes in the dark, by which time the insects have completely recovered from the anaesthetic effects. Bennitt and Merrick (1932) have reported a comparable result in Crustacea due to crowding, which they associate with oxygen lack.

The Effects of Operative Techniques

With carefully sharpened No. 12 hard steel needles an incision was made in the head capsule on the side of the frons along the ocular suture where the cuticle is easily punctured. From this approach the optic tract can be severed. Twenty moths were successfully operated upon in this way, and lived at least four days thereafter. It is of interest to note that an operation of this kind apparently releases the female from certain inhibitions to oviposition, for eggs were deposited in the vials far more frequently by operated than by control females. Several

operations did not completely sever the optic tract, and the results of such cases constitute controls. In every case in which the nerve fibers were completely severed, the pigment in that eye was in the light-adapted position, irrespective of the position of the pigment in the eye on the uninjured side. Moreover, once the pigment was brought into the light position by cutting the optic tract, it could never be caused to migrate back to the dark position, although appropriate methods (heat, ether, dark, etc.) were employed. Thus Fig. 12 shows a section of the head of an insect which had been kept for four days in the dark after an operation had been performed on the left eye (left side of the illustration). The pigment cells on the unoperated side occupy the extreme dark position, while those on the operated side have taken up positions characteristic of cells released from their usual control, i.e., they have migrated further proximally than they would under normal light conditions, and their movement is somewhat irregular. The difference between two such eyes can be detected in the living moth.

DISCUSSION

Two of the above experiments provide strong evidence against a hormonal control of movement. The effect of short exposures of light on a small number of ommatidia results in the movement of only a few pigment cells. A hormone in the blood stream would be more general in its action. But this experiment does not differentiate between a nervous control and the possibility that the cells behave as independent effectors. This latter possibility is shown to be untenable, however, by the results of cutting the optic tract, which also provides further evidence against the theory of humoral control, since the blood supply to the eye on the injured side is in no way impaired. There remains only the theory of the nervous control of pigment migration.

The absence of diurnal rhythms of migration does not argue against the nervous control, and neither do the effects of light. The rate of movement is admittedly slow compared with speed of muscular movements in insects, but the movement does not appear to be muscular in nature. Reasons have been given above for discounting the evidence concerning the apparent absence of a nerve supply to the pigment cells. The remote possibility of the liberation of the appropriate chemical mediator occurring as the result of antidromic impulses along the sensory nerves should not be overlooked.

The action of chloretone, carbon dioxide, light, and low temperature would be interpreted on the nervous theory as agents which cause cessation or decrease of impulses from the brain which normally maintain

the pigment cells in the dark position. There is actually no positive evidence in favor of the nervous control since no method has been found for any arthropod which induces movement into the dark position, except darkness itself.

In addition, it has been shown in the above experiments that changes in the phototactic behavior of *Ephestia* are not entirely dependent upon the position of the accessory pigment cells. Nevertheless, the variation in the position of the pigment should be considered in investigations on the behavior such as that of Brandt (1934), and may explain some of the irregularities which he reported. Likewise, the results reported by Taylor and Nickerson (1940) on changes in retinal potentials during light adaptation should also be considered in relation to the pigment migration which doubtless occurs in *Galleria* as in *Ephestia*. The possibility of relating electrical response to migration of eye pigments has already been suggested in the case of some beetles by Jahn and Crescitelli (1940).

SUMMARY

The accessory pigment cells in the eyes of *Ephestia kuehniella* migrate from their distal position between the cones to a more proximal position when exposed to light of sufficient intensity.

A comparable, or even more marked, effect is produced by low temperatures, chlorotone, high tensions of carbon dioxide, and by cutting the optic tract.

Movement of individual cells can be induced by illuminating only a few of the ommatidia. This suggests that a hormonal method of control is unlikely. The fact that pigment cells can never be induced to migrate into the dark position once the optic tract has been severed suggests that the cells do not respond as independent effectors.

In view of these several lines of evidence, though most of it is admittedly negative, it is possible that the migration of the accessory pigment cells in the eyes of *Ephestia* may be principally controlled by a nervous mechanism. It should again be emphasized that any conclusions based on the study of moths cannot necessarily be applied to other insects, let alone to Crustacea.

LITERATURE CITED

- BENNITT, R., 1924. The migration of the retinal pigment in crustaceans. *Jour. Exper. Zool.*, **40**: 381-435.
—, 1932. Physiological interrelationship in the eyes of decapod crustacea. *Physiol. Zool.*, **5**: 49-64.
BENNITT, R., AND A. D. MERRICK, 1932. Migration of the proximal retinal pigment in the crayfish in relation to oxygen deficiency. *Biol. Bull.*, **62**: 168-177.

- BRANDT, H., 1934. Die Lichtorientierung der Mehlmotte *Ephestia kuehniella* Zeller. *Zeitschr. vergl. Physiol.*, **20**: 646-673.
- BROWN, F. A., AND A. MEGLITSCH, 1940. Comparison of the chromatophorotropic activity of insect corpora cardiaca with that of crustacean sinus glands. *Biol. Bull.*, **79**: 409-418.
- COLLINS, D. L., 1934. Iris-pigment migration and its relation to behavior in the codling moth. *Jour. Exper. Zool.*, **69**: 165-198.
- CONGDON, E. D., 1907. The effect of temperature on the migration of the retinal pigment in decapod crustaceans. *Jour. Exper. Zool.*, **4**: 539-548.
- CORTEGGIANI, E., AND A. SERFATY, 1939. Acétylcholine et cholinestérase chez les Insectes et les Arachnides. *Compt. Rend. Soc. Biol.*, **131**: 1124-1126.
- CROZIER, W. J., E. WOLF, AND G. ZERRAHN-WOLF, 1937. Critical illumination for response to flickered light, with dragonfly larvae (*Anax*), in relation to area of eye. *Jour. Gen. Physiol.*, **21**: 223-247.
- DEMOLL, R., 1911. Über die Wanderung des Irispigments im Facettenauge. *Zool. Jahrb. Abt. Allg. Zool. u. Physiol.*, **30**: 169-180.
- , 1917. Die Sinnesorgane der Arthropoden, ihr Bau und ihre Funktion. 243 S. Braunschweig, 1917.
- EPHRUSSI, B., AND G. W. BEADLE, 1936. A technique of transplantation for *Drosophila*. *Am. Nat.*, **70**: 218-225.
- EXNER, S., 1891. Die Physiologie der facettierten Augen von Krebsen und Insekten. 206 S. Leipzig u. Wien, 1891.
- FRIZA, F., 1928. Zur Frage der Färbung und Zeichnung des facettierten Insektenauges. *Zeitschr. vergl. Physiol.*, **8**: 289-336.
- HANSTRÖM, B., 1937. Vermischte Beobachtungen über die chromatophoraktivierenden Substanzen der Augenstiele der Crustaceen und des Kopfes der Insekten. *Kungl. Fysiogr. Sällsk. Handl. Lund*, **47**: 1-10.
- HORSTMANN, E., 1935. Die tagesperiodischen Pigmentwanderungen im Facettenauge von Nachschmetterlingen. *Biol. Zbl.*, **55**: 93-97.
- JAHN, T. J., AND F. CRESCITELLI, 1940. Diurnal changes in the electrical response of the compound eye. *Biol. Bull.*, **78**: 42-52.
- KLEINHOLZ, L. H., 1936. Crustacean eye-stalk hormone and retinal pigment migration. *Biol. Bull.*, **70**: 159-184.
- , 1938. Studies in the pigmentary system of Crustacea. IV. The unitary versus the multiple hormone hypothesis of control. *Biol. Bull.*, **75**: 510-532.
- MERKER, E., 1929. Einfache Praktikumversuche zur Beobachtung der Pigmentwanderung in den Augen von Tagfaltern und Dämmerungsschmetterlingen. *Biol. Zbl.*, **49**: 186-191.
- PARKER, G. H., 1932. The Movements of the Retinal Pigment. *Ergebn. Biol.*, **9**: 239-291.
- PEABODY, E. B., 1939. Development of the eye of the isopod, *Idothea*. *Jour. Morph.*, **64**: 519-554.
- ROEDER, K. D., 1939. The action of certain drugs on the insect central nervous system. *Biol. Bull.*, **76**: 183-189.
- SNODGRASS, R. E., 1935. Principles of Insect Morphology. McGraw-Hill, N. Y.
- TAYLOR, I. R., AND M. NICKERSON, 1940. Potential changes in the eye of the moth, *Galleria mellonella*, during the course of dark adaptation. *Anat. Rec. Suppl.* **78**: 92.
- UCHIDA, H., 1934. Color changes in the eye of a long-horned grasshopper, *Homoeropyphus lineosus*, in relation to light. *Jour. Fac. Sci. Univ. Tokyo*, **3** (3): 517-525.
- UMBACH, W., 1934. Entwicklung und Bau des Komplexauges der Mehlmotte *Ephestia kuehniella* Zeller nebst einigen Bemerkungen über die Entstehung der optischen Ganglien. *Zeitschr. Morph. Ökol. Tiere*, **28**: 561-594.

- WELSH, J. H., 1930. The mechanics of migration of the distal pigment cells in the eyes of *Palaemonetes*. *Jour. Exper. Zööl.*, **56**: 459-494.
- , 1935. Further evidence of a diurnal rhythm in the movement of pigment cells in eyes of crustaceans. *Biol. Bull.*, **68**: 247-252.
- , 1938. Diurnal Rhythms. *Quart. Rev. Biol.*, **13**: 123-139.
- , 1939. The action of eye-stalk extracts on retinal pigment migration in the crayfish, *Cambarus bartoni*. *Biol. Bull.*, **77**: 119-125.
- , 1941. The sinus glands and 24-hour cycles of retinal pigment migration in the crayfish. *Jour. Exper. Zööl.*, **86**: 35-50.
- VON DER WENSE, T. F., 1938. Wirkungen und Vorkommen von Hormonen bei wirbellosen Tieren. Leipzig, 1938.
- WIGGLESWORTH, V. B., 1939. The Principles of Insect Physiology. Methuen, London.